Further observations of visual signalling in Australo-Papuan hylid frogs of the genus *Litoria* (Tschudi)

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Introduction

Intra-specific communication in anuran amphibians is primarily achieved with vocal signals (Duellman and Trueb 1994). However, some species also use visual displays for inter- and/or intra-sexual communication (Hödl and Amezquita 2001). Such displays include movement of the fore and/or hindlimbs (e.g. hand-waving, foot-flagging and/or leg-flicking), movement of the body or posturing, and exhibition of a brightly coloured vocal sac (Hödl and Amezquita 2001; Hirschmann and Hödl 2006). Visual signalling is hypothesised to be an alternative or complementary mode of communication in anurans used under certain environmental and/or social conditions (e.g. in noisy or visually complex environments) (Amezquita and Hödl 2004).

To date, visual signalling involving limb movements has been described in few anuran species. The most recent review of visual signalling in amphibian species (Hödl and Amezquita 2001) reported this behaviour in just 13 frog species globally from eight genera, including four Australo-Papuan hylid frogs from the genus *Litoria* namely: *L. nannotis, L. rheocola, L. genimaculata* (now *L. serrata* [Richards *et al.* 2010]) and *L. fallax.* Visual displays in these species of *Litoria* include leg-flicking as well as slow deliberate movements of the hindlimbs (e.g. extension of the hindlimbs outwards and/or backwards) (Richards and James 1992).

This paper presents observations of hand-waving, foot-flagging and leg-flicking semaphore behaviour in another three *Litoria* species: *L. pearsoniana* and *L. cooloolensis* from eastern Australia, and *L. iris* from Papua New Guinea. Additional observations of visual displays in *L. fallax* (including foot-flagging and leg-flicking) are also provided.

Hand-waving and leg-flicking behaviour in the cascade treefrog *Litoria pearsoniana*

On 23 January 2009, one of us (KM) observed hand-waving and leg-flicking behaviour in *L. pearsoniana* along a section of Roland's Creek in Mount Jerusalem National Park (NP), north-east New South Wales (28° 29´ S; 153° 22´ E 220 m asl). At this location, Roland's Creek is a small, rocky stream fringed by riparian rainforest. At the time of observation (~2215 hours), the stream was shallow and flowing slowly, forming quiet riffles in the rocky sections interspersed by pools. The temperature was warm (~23 °C), there was substantial cloud cover due to the presence of large storm clouds and there was negligible moonlight (near new moon). The animals seen displaying (approximately 10 different individuals) were amongst 15 calling male *L. pearsoniana* encountered along a short section of creek (~50 m) within a 100 m survey transect. No other frog species were calling or observed at this site at the time.

Interacting *L. pearsoniana* males were calling and displaying at numerous sites along the stream, up to ~1 m above the streambed, and perched on rocks, low tree branches or leaves and exposed roots on eroded stream banks. Visual displays accompanied vigorous calling and comprised flicking or lifting of any of the four limbs. Each flick was very rapid lasting only a fraction of a second. In some cases, more than one limb was flicked simultaneously (e.g. left hand/right foot). The visual signals were in some cases clearly directed towards neighbouring males within close proximity (0.5-2 m) of the signaller, but in other cases no specific receiver could be detected. No physical contact occurred during these displays.

Over a video-sampled period of 1 minute, a male signalling acoustically and visually to a neighbouring male approximately 1 m away (also visually displaying) executed 26 limb-flicks, comprising two left hand, five left foot, eight right hand and 11 right foot flicks. In addition, the male executed a left foot lift (not including extension of the limb), a simultaneous left foot/right foot lift movement, a left hand/right foot flick movement, a right hand/left foot flick movement and a right foot-flag/body turn movement. Similar movements were observed in the other visually displaying individuals, but these were not quantified.

EM has observed similar behaviour in male *L. pearsoniana* along streams in the D'Aguilar Range and on Lamington Plateau, south-east Queensland. In both areas, male

L. pearsoniana were seen engaging in leg-flicking behaviour when in close proximity to other calling males on spring and summer nights with heightened calling activity (i.e., with the formation of calling aggregations of 5-6 male *L. pearsoniana* over 20 m or less of stream transect). Few if any other frogs were heard calling at the time when *L. pearsoniana* were seen displaying. On Lamington Plateau, foot-flicking behaviour was elicited through imitation or playback of calls of male *L. pearsoniana.* Here densities of calling male *L. pearsoniana* were lower (circa. 1-4 animals per 20 m of stream).

Foot-flagging behaviour in the Cooloola sedgefrog *Litoria cooloolensis*

Observations of foot-flagging in *L. cooloolensis* were made by EM at Lake Poona, Cooloola NP, south-east Queensland (25°58´ S 153° 07´ E) on 29 January 2000. The observations were made on a still, cloudless and moonless night with the ambient temperature about 22 °C. The site supported a high density of male *L. cooloolensis* (>2 individuals per m^2) with the majority calling from sedges. At the start of observations (~ 2000 hours) two male *L. cooloolensis* were seen perched on the trunk of an emergent paperbark (*Melaleuca quinquenervia*) tree, approximately 0.5 m apart, within 1.0 m of the water's surface. Both frogs were calling, with calls of the first (higher) male noticeably louder than calls of the second (lower) and calls of other male *L. cooloolensis* calling from emergent sedges nearby (within 1-5 m of the aforementioned frogs). Shortly after commencing observations, the second male calling from the base of the tree moved up the trunk towards the first (louder) male. When approached, the first male extended its left leg outwards (i.e., laterally) and backwards in a 90° arc. At the completion of the arc, the leg was left dangling for several seconds before being drawn back alongside the body. The same process was then repeated with the right leg. When extended backwards, both legs were trembling slightly with the pale underside of the feet clearly visible. This display was repeated as the second male continued to approach the first. This time, however, both the left and right legs were left dangling behind the body for several seconds. As before, both legs were seen trembling at this time. During the display, both frogs continued calling normally. After the second display, the second frog jumped upon the first and the two began wrestling. After approximately two minutes, the frogs separated, coming to rest a short distance apart. Having separated, both frogs began foot-flagging, alternately extending left and right legs and briefly holding each leg behind them in the manner described above. Both frogs continued to produce typical calls. After displaying to each other, the two frogs briefly resumed fighting until the second frog leapt into the water. The first male remained perched and continued calling thereafter. Observations ceased at ~ 2005 hours.

Leg-flicking behaviour in *Litoria iris,* Papua New Guinea

Observations of foot flagging by an adult male *L. iris* were made by HH on 21 March 1998 near Haia in Chimbu Province of Papua New Guinea (6° 45´ S 145° 03´ E). During the afternoon, heavy rain had fallen resulting in flash flooding of streams. In the early evening a single male *L. iris* was heard calling beside a small, slow moving stream. When this call was imitated, the male threw out a hindlimb briefly, flashing the bright red coloration of the posterior surface of the thigh and the under-side of the foot. This behaviour was repeated several times in response to imitated calls, being predictable enough to enable it to be photographed (Figure 1A). No other frogs were heard calling from this stream section during these observations.

Foot-flagging and leg-flicking behaviour in the eastern sedgefrog *Litoria fallax*

EM has observed foot-flagging behaviour similar to that of *L. cooloolensis* (i.e., extension of the hindlimbs backwards and outwards in an arc and trembling of the hindfeet) in calling male *L. fallax* at a pond in Karawatha Forest, south-east Queensland (27° 38´ S 153°05' E) (Figure 1B and 1C). This behaviour was observed during spring and early summer, on nights with especially high densities (up to 6 animals per m^2) of calling male *L. fallax*. On these same nights, a number of other frog species (*Litoria gracilenta*, *L. dentata*, *L. caerulea*, *Limnodynastes peronii* and *Platyplectrum ornatum*) were also calling strongly. At Karawatha Forest, foot-flagging was observed across a range of temperatures with variable cloud cover and ambient (moon) light (Table 1).

In addition to foot-flagging, calling male *L. fallax* were seen to engage in rapid flicking of the hindlimbs, similar to that described in *L. pearsoniana* above. On nights when foot-flicking was observed, fighting between male *L. fallax* was frequent. In most cases foot-flicking was seen to precede fighting, with animals jumping on top of and kicking one another.

Discussion

Visual displays like those described here have previously been reported in *Litoria* species associated with fast-flowing rainforest streams (*L. seratta*, *L. rheocola* and *L. nannotis*) and *L. fallax*, a pond-breeding species from coastal eastern Australia (Richards and James 1992). The agonistic foot-flagging behaviour of male *L. cooloolensis* (a pond-breeding species) described here is very similar to that described previously in the closely-related *L. fallax* by Richards and James (1992). In addition to the foot-flagging behaviour described by Richards and James (1992), we have observed male *L. fallax* engaging in visual displays involving rapid flicking of the hindlimbs when interacting with conspecific males. As reported here, similar leg-flicking behaviour also occurs in *L. pearsoniana*.

When describing the foot-flagging behaviour of *L. fallax*, Richards and James (1992) questioned whether this behaviour was influenced by ambient light (i.e., moonlight). Our observations suggest this is not necessarily the case with foot-flagging behaviour recorded on nights with little or no moonlight and nights with bright moonlight. Similarly, previous authors have suggested that visual signalling should be most prevalent in diurnal species and/or augment communication in visually or acoustically challenging environments, such

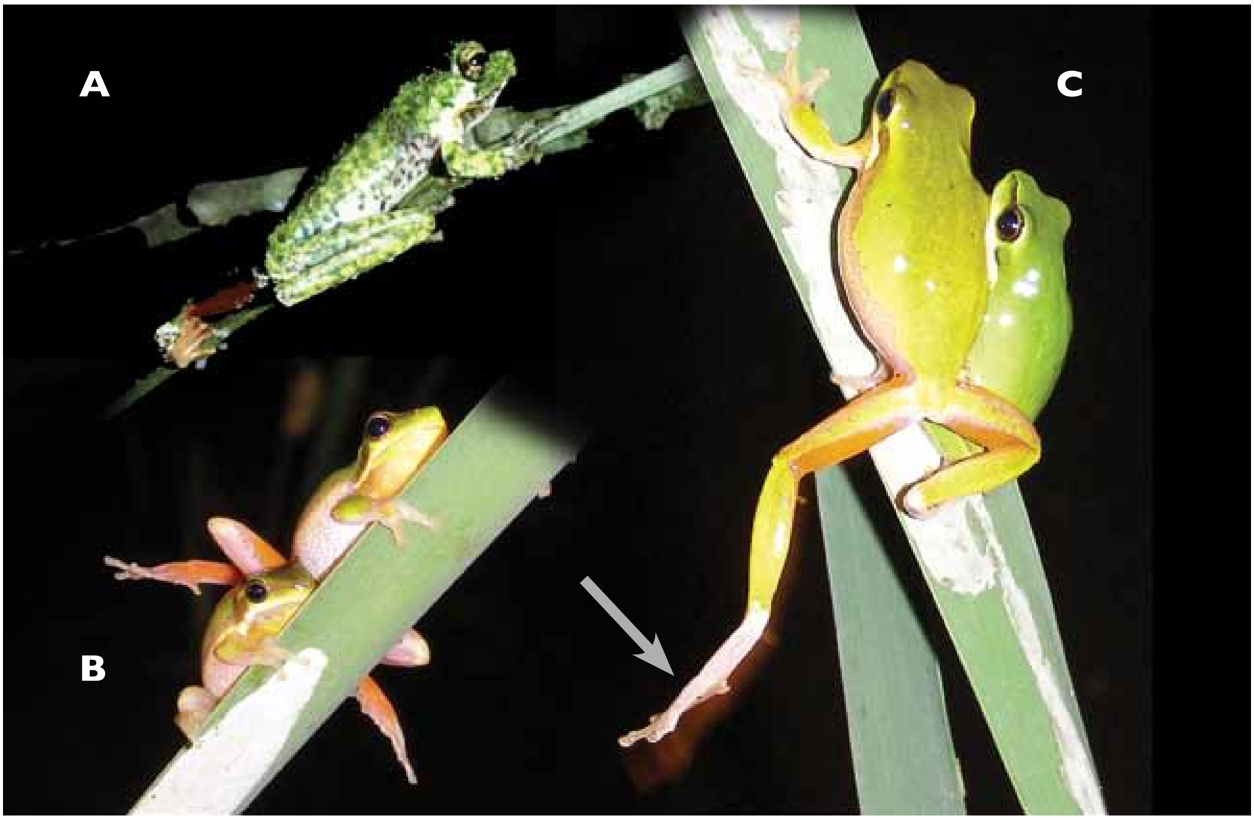

Figure 1. (A) Male *Litoria iris* displaying brightly coloured feet and thighs, Chimbu Province, Papua New Guinea. (B) Agonistic interaction between foot-flagging male *L. fallax* at Karawatha Forest, south-east Queensland. (C) Foot-flagging male *L. fallax* at Karawatha Forest with hind left leg fully extended and second calling male (the aggressor in this interaction) nearby. Note that the ghosting/blurring highlighted by the arrow in (C) is the result of trembling of the hind left foot. Photos, (A) H. B. Hines and (B and C) E. Meyer.

Table 1. Conditions under which calling male *Litoria fallax* were observed engaging in foot-flagging and leg-flicking behaviour at Karawatha Forest, south-east Queensland. NR = not recorded.

Date	Time	Air temperature (°C)	Moon rise	Moon set	Moon phase	Cloud cover (eighths)	Rainfall in previous 24 h	Breeding activity recorded
5/1/2008	2130	23.3	0146	1612	Near new	8	Yes	Yes
27/1/2007	0330	26	1329	-	Near full	8	Yes	Yes
4/12/2007	NR	NR	0645	2126	Near new	NR	Yes	Yes
27/10/2005	2030	19	1715	0420	Near full	0	Yes	Yes

as noisy streams (Amezquita and Hödl 2004). Our observations of visual signalling in *L. cooloolensis* and *L. fallax* on nights with high levels of background noise, from calling conspecifics and/or other frog species, accord with this view. Observations of visual display by *L. pearsoniana* and *L. iris* along quiet streams with very little background noise, however, suggest other factors may also be at play. With calling being highly energetically expensive (Pough et al. 1992), visual signalling could perhaps provide a less costly means of male-male communication (in which case visual signalling may represent an evolutionary response to energetic demands associated with calling). Data comparing the energetic cost and efficiency of different signalling strategies in *L. pearsoniana* and/or *L. iris* are needed to investigate this hypothesis further.

Our observations and those of previous authors (reviewed by Hödl and Amezquita 2001) indicate that visual displays involving the movement of limbs, such as foot-flagging, occur in more anuran species than previously documented. Observations reported here show that visual signalling occurs across a much broader range of conditions than previously thought, indicating that this form of communication in anuran amphibians may have evolved in response not only to high levels of background noise, but other factors as well. More systematic and detailed behavioural studies are required to confirm this and to understand better the evolution of such behaviour in anuran amphibians. Further study and reporting of visual displays in anuran species are therefore to be encouraged.

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